Tropical forests in the Americas are changing too slowly to track climate change

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Abstract: Understanding the capacity of forests to adapt to climate change is of pivotal importance for conservation science, yet this is still widely unknown. This knowledge gap is particularly acute in high biodiversity tropical forests. Here we examine how tropical forests of the Americas have shifted community traits composition in recent decades as a response to changes in climate. Based on historical trait-climate relationships we found that, overall, the studied functional traits show shifts of less than 8% of the expected shift given observed changes in climate. However, the recruit assemblage shows shifts of 21% relative to climate change expectation. The most diverse forests on Earth are changing in functional trait composition, but at a rate that is fundamentally insufficient to track climate change.

One-Sentence Summary: The trait composition of tropical forests in the Americas is changing but not fast enough to keep track of climate change.

Main Text

Forest responses to human-driven perturbations, such as climate change, will largely determine the diversity and function of the terrestrial biosphere through this century and beyond. Tropical forests in the Americas host the greatest concentration of tree species in the world (*1*), including six key biodiversity hotspots (*2*) and half of Earth's most intact tropical forests (*3*). In the face of threats from climate change and continuing loss in area and integrity (*3, 4, 5, 6*), it is both critical and urgent to understand the ability of these complex systems to adapt to change and survive.

Within tropical American forests (referring to all forests encompassing continental areas from Brazil to Mexico), lowland forests provide relatively homogenous climatic conditions over large areas, potentially allowing the existence of common functional adaptations over large spatial extents. In contrast, across mountain forests climatic conditions tend to change rapidly in space, potentially facilitating rapid turnover of functional adaptations to local environmental conditions. In Amazonia, changes in precipitation patterns and more frequent droughts have led to an increase in the recruitment of dry-affiliated species (xerophilization) (*7*). In the Andes, rising temperatures have led to increasing abundances of species tolerant to higher temperature (thermophilization) (*8*). Across Mesoamerica it is expected that climate change will cause an expansion of tropical dry forests to higher elevations (over 200 m above current average elevation) (*9*). However, tree species may be unable to shift their distribution fast enough to track their climatic niche, given their slow demography (e.g. growth and recruitment), the prevalence of dispersal limitation (*10*) and different environmental tolerances at different life stages *(11)*. All these limitations would increase the vulnerability of tree species to climate change across tropical American forests. For instance, in higher latitudes recent work has shown large range contractions of tree species rather than range expansions or shifts (*12*). Changes in climate across the tropical Americas are expected to become stronger, with some scenarios projecting temperature increases of up to ~4°C and precipitation reductions close to 20% by 2100 (*13, 14, 15*). This would likely increase the vulnerability of current tree species assemblages as they would face climates they have not previously experienced (*16*), potentially selecting for no-analog future plant communities (*17*).

Functional traits mediate species responses to environmental change, impacting plant performance and species distributions (18*, 19, 20*). These morphological, structural, chemical, and phenological characteristics tend to show consistent relationships with climate and soil conditions (*21*). Recent work has shown positive relationships between mean annual temperature and leaf area, specific leaf area, leaf nitrogen, wood density and leaf thickness (*22*) depicting plant functional adaptations to local environmental conditions. Other work has detected a negative relationship with elevation for specific leaf area and leaf nitrogen, potentially as adaptation to cooler environments with lower nutrient availability (22). Hence, these traits are tightly linked to the capacity of species to respond to environmental changes. For instance having large area can increase leaf temperature due to higher solar absorption, while smaller leaves dissipate heat more effectively and help avoid water losses. Plants with lower specific leaf area, i.e. with thicker and tougher leaves, tend to be more resistant to drought as these can better resist water loss. High wood density is tighly related to increased resistance to cavitation which can increase their capacity to survive droughts. Therefore, a trait-based approach provides a promising framework for predicting the impacts of climate change and resilience across forest ecosystems (*19, 23, 24*).

It is still unclear how shifts in the abundance and distribution of species translate into changes in the functional trait composition, and what functional changes have occurred through the last half century as a response to the onset of a warmer, drier and more variable climate across the tropical Americas. Moreover, it is unknown if forest-level functional shifts are more attributable to differential growth among the surviving trees than to the addition (i.e. recruitment) or removal (i.e. mortality) of trees to the assemblage. It is also uncertain if these functional shifts match the direction of climate change, and if so, whether the rate of functional trait change keeps pace with climate change or lags behind. Understanding the above will allow the quantification of the present, and likely future, capacity of forest to adapt to a changing climate and to uncover which functional trait characteristics may confer forests higher adaptation capacity to a changing climate.

Here, we address these knowledge gaps by analysing 415 long-term forest plot sites monitored over more than 40 years (1980 - 2021). This dataset includes information on the identity, size, recruitment and mortality of >250,000 individual trees across the tropics from Mexico to southern Brazil. Our effort spans relatively undisturbed forests from the lowland tropics (hereafter forest plots <700 m elevation) to pre-montane and montane zones (>700 m elevation; henceforth referred to as montane) from the Andes to subtropical fringes (Fig. 1; data S1). These forests are distributed along a wide range of climatic and soil conditions (Fig. 1B) and have experienced strong changes in climate over the past decades (Fig. 1C). We combine this monitoring and analysis of changes in the plant community composition with measurements of 12 plant functional traits that are potentially involved in responses to a changing climate. These include photosynthetic capacity (A_{sat}), leaf chemistry (content of carbon: C, nitrogen: N and phosphorus: P), leaf area (Area), specific leaf area (SLA), leaf fresh mass (FM), leaf thickness ("Thickness"), abundance of deciduous species (DE), adult maximum height (H_{max}), wood density (WD) and seed mass (SM) (table S1). Tree functional trait data were obtained for several plots from local field collections carried out by collaborators (*25, 26, 27*), the Global Ecosystems Monitoring network (GEM; gem.tropicalforests.ox.ac.uk) (*28*), and ForestPlots (www.ForestPlots.net) (*29*) in addition to databases from BIEN (bien.nceas.ucsb.edu), TRY (www.try-db.org) (*30*) and Díaz et al. (*19, 31*).

We first investigate long-term plant trait-environment relationships to understand how climate drives trait distributions in tropical forests of the Americas and if these relationships are consistent across lowland and montane forests. We expect temperature and water availability to be the main drivers of plant trait distributions, with warmer and drier areas facilitating the dominance of more conservative trait syndromes (e.g. smaller and thicker leaves, higher wood density, lower photosynthetic capacity) in comparison to warm and wetter areas *(32, 33)*. Moreover, we expect trait-environment relationships to differ between lowland and montane forests given the different climatic ranges of these forest types.

We then examine how and where lowland and montane tropical American forests have shifted in their functional trait composition due to changes in the plant community taxonomic composition over the last four decades. We do this by analysing the annual rate of change (Δr) of the trait community-weighted mean (CWM) for all forests (lowland and montane together) and for lowland and montane forest separately. Because of the long lifespan of tropical trees (*34*) and their slow turnover, we performed this analysis at the full community level and separately for the recruiting ('recruit'), mortality ('fatality'), and surviving (here onwards 'survivor') assemblages (Fig. 2). Analysing changes at the full community level (involving all trees >10 cm DBH alive) allows us to understand how communities are changing in their trait CWM given tree growth, survival and recruitment together. Analysing the survivor (change in CWM given by growth) assemblage alone will allow gaining insights into potentially more resistant trait values, while analyses for the fatality assemblages will identify potentially less resistant trait values. The recruit community will impact the full community level trait composition dependent on their basal area and will provide information on potentially better adapted trait values to the current climate that allow them to recruit into the community, as well as indicate the possible composition of future forests.

We further analysed if observed changes in trait composition have been enough to track climate change to date by comparing observed and expected trait changes based on historical trait-environment relationships (see materials and methods *(35)*). This climate change tracking analysis was carried out for the full community, survivor and recruit assemblages but not for the fatality assemblage because these individuals will not contribute to future change (Fig. 2).

Given exposure to a drying and warming climate, we could reasonably expect increased abundance of species exhibiting more drought-tolerance traits (i.e. in the 'slow' section of the plant economics spectrum) (*36*), such as high wood density (e.g. to prevent cavitation) (*37*) and smaller, thicker leaves (e.g. for lower evapotranspiration and reduced radiation exposure) *(38)*. However, it's also possible that increasing drought will drive a shift toward drought-avoidance traits, notably deciduousness (often associated with more acquisitive leaves) (*32, 39*). Seed traits play a pivotal role in the reproduction and dispersal capacity of species (*40*). Under an unstable, warming and drying climate, we might expect species with smaller wind-dispersed seeds to increase in abundance *(41)*. This is because wind-dispersed seeds, which are more common in drier and more seasonal biomes, tend to be smaller than animal-dispersed seeds (*42*). However, other factors, such as wind and fire disturbance, defaunation of frugivorous seed-dispersing mammals and birds, may disrupt the expected trends in seed traits as these drive more strongly their shifts at short time scales than a changing climate (*43*). If migration is an important component of species response to climate change, we would also expect montane forests to show stronger functional responses than lowland forests given their more varied climatic conditions at shorter distances (*8, 33*), which make it potentially easier to migrate to a favorable climate than in the lowlands (*44, 45, 46, 47*). In montane forests, nutrient availability (e.g., N:P ratios) can vary significantly along altitudinal gradients due to substantial changes in temperature and water availability (*48*). As a result, we expect strong functional responses to soil nutrient availability across these elevation gradients.

We expect that, given the long lifespan of tropical trees and rapid pace of recent climate change, forests will show ecological inertia, so that changes in functional composition lag behind changes in climate. We expect the full community and survivor assemblages to show slower change given their change is largely dependent on tree growth, which is a slow process among tropical forests trees. The recruit and fatality assemblages may show faster and larger community trait responses as they are less dependent on growth and more dependent on local climate conditions.

Long-term trait-environment relationships

To evaluate long-term (1980-2021) trait-climate relationships across tropical American forests, we used data from 415 forest plots (mean plot size 0.88 [min: 0.12, max: 25] ha and 5.7 [min: 2, max: 41] censuses per plot), for which we extracted climate (*49*) and soil *(50)* data for their sampling years. As species' contributions to ecosystem processes likely depend on their relative abundances (*51*), we calculated the community-weighted mean of each plant functional trait (table S1) for each plot based on the relative basal area of the species and their trait value (hereafter "community functional traits"). The trait values were obtained from the sources mentioned above (*19, 25, 26, 27*, *28*, *29*, *30, 31*). We then modelled each community functional trait as a function of the additive effects of relevant and largely uncorrelated climatic drivers of species distributions (Fig. S1), i.e., the mean annual values of temperature (T_{mean}), vapour pressure deficit (VPD_{mean}) (*52*), maximum climatic water deficit ($MCWD_{mean}$) (*53*) and standardised precipitation-evapotranspiration index ($SPEI_{12}$) (*54*), each one of these interacting with forest type (lowland or montane). As soil characteristics can impact plant distributions (*24*), we included cation exchange capacity (CEC), pH, and the percentage of clay and sand for each plot location in the models (see materials and methods *(35)*). We accounted for differences in the number of censuses, plot size and census time per vegetation plot and for the potential spatial autocorrelation.

Several community functional traits show consistent relationships with climate across forest type (table S2; Fig. S2), with temperature showing some of the strongest effects driving plant trait distributions across lowland and montane forests (Fig. 3). As expected, an increase in temperature (T_{mean}) across space is associated with an increase in community-mean leaf area and seed mass, and a decrease in photosynthetic capacity, specific leaf area, and the proportion of deciduous species across lowland and montane forests. Moreover, an increase in water stress ($MCWD_{mean}$) is associated with decreases in specific leaf area and adult maximum height for both forest types (table S2; Fig. S2). This represents an increase in the conservative trait strategy linked to more extreme conditions.

However, the relationship with temperature is not consistent across lowland and montane forests for leaf chemistry (leaf carbon, nitrogen and phosphorus content), wood density, adult maximum height, leaf fresh mass or leaf thickness (Fig. 3). An increase in water stress ($MCWD_{mean}$) is associated with an increase in photosynthetic capacity, leaf nitrogen content, leaf area and wood density across lowland forests but decreases in montane forests (table S2; Fig. S2). The increase in these leaf traits in drier forests could be associated with the high photosynthetic rates generally attained by deciduous species over the growing season (*55, 56*) and the fact that lower adult maximum height and higher wood density tend to correlate with higher resistance to lethally low levels of soil moisture availability (*57*). However, consistent climatic relationships across both forest types are not apparent for the other traits analysed (table S2; Fig. S2). One plausible explanation is that this reflects their different position along the climatic gradient (i.e. temperature and precipitation), with lowlands occupying areas with more homogeneous climate conditions across large spatial extents in comparison to montane forests, which span a large range of climates across smaller spatial extents.

Changes in trait composition across time

We next asked if and how the functional trait composition of tropical American forests has shifted, and how much of this can be explained by observed changes in climate over the past 40 years. We first calculated the community-weighted mean (CWM) of each plant functional trait for each vegetation census available for full community assemblage, and separately for the survivor (individuals that are alive in two subsequent censuses, e.g. from census one to census two), recruit (individuals not present in the previous census and recruited in the subsequent census) and fatality (individuals alive in previous census but dead in the subsequent census) assemblages. We define the recruit assemblage as individuals that passed the threshold of 10 cm DBH between one census and the next. Then we calculated their yearly rate of change across time. We tested if the changes in trait CWM differed from zero across all vegetation plots, with plots separated into lowland and montane forests. We calculated the Highest Density Interval (HDI) containing the 95% most probable effect values and considered it significant when the HDI did not overlap 0. We then investigated whether the observed shifts in trait CWM differed significantly between lowland and montane forests. For shorthand and readability, all mention of mean traits and shifts below refer to CWM trait values.

When considering all plots together for the full community assemblage, we found that seven out of the 12 traits analysed exhibited significant changes in their CWM values (Fig. S3; see Fig. 4 for trait changes across assemblages). Only leaf nitrogen, fresh mass, specific leaf area, seed mass and wood density did not show significant shifts across time (table S3; Fig. S4). The survivor assemblage showed the same pattern of community trait changes (table S3; Fig. 5) as the full community assemblage, with the main differences being a significant decrease in leaf fresh mass in the lowlands for the survivor assemblage. Hence, hereafter we focus on the results from the survivor, recruit and fatality assemblages. Overall, we found larger variation in trait CWM across space (i.e. with geographical variation in climate) than across time. For the community traits with significant changes for the survivor assemblage, we found an average increase in photosynthetic capacity of 0.0023 μmol m^{-2} s^{-1} $year^{-1}$ (HDI-low and HDI-high: 0.0007, 0.0038), leaf carbon content 0.0011% $year^{-1}$(0.0004, 0.0019), phosphorus 1.6×10^{-5}% $year^{-1}$ (5.7×10^{-6}, 2.7×10^{-5}), the abundance of deciduous species 0.03 % $year^{-1}$ (0.01, 0.05) and adult maximum height 0.006 m $year^{-1}$ (0.002, 0.009), while community leaf area decreased on average -0.03 cm^2 $year^{-1}$ (-0.06, -0.007) and leaf thickness decreased -0.05 mm $year^{-1}$ (-0.08, -0.02) (Fig. 5; table S3). In the lowland forests, we detected significant trait changes for six (increasing: photosynthetic capacity, leaf carbon content, adult maximum height and abundance of deciduous species; decreasing: leaf area and fresh mass) out of the 12 traits analysed (table S3; Fig. 5). Montane forests showed significant, but rather small, increases in leaf carbon, phosphorus and the abundance of deciduous species (table S3; Fig. 5).

The recruit assemblage experienced significant changes for seven traits, with six showing decreases, i.e. leaf carbon content -0.014% year^{-1} (-0.02, -0.001; in montane forests), leaf nitrogen content -0.002% year^{-1} (-0.004, -0.0002), leaf thickness -0.04 mm year^{-1}(-0.08, -0.01), deciduousness -0.17 % year^{-1} (-0.33, -0.02), adult maximum height (-0.03 m year^{-1} [-0.07, -0.003], and WD: -0.0007 g cm^3 year^{-1}). The leaf fresh mass of recruits increased on average 0.04 g year^{-1} (0.006, 0.08; Fig. 5; table S3). For the fatality assemblage, only the CWM of leaf nitrogen content -0.004 % year^{-1} (-0.007, -0.001; montane forests), leaf fresh mass, -0.02 g year^{-1} (-0.05, -0.0003) and seed mass -17.7mg year^{-1} (-29.9, -5.7) in lowland forests experienced significant declines (Fig. 5; table S3).

To help identify the underlying climatic drivers of forest functional change, we used multivariate linear models to estimate the yearly change (Δr; i.e. from first to last census), in the trait values (Δ_r trait CWM) as a function of the yearly rate of change in temperature (ΔT_r), maximum climatic water deficit (ΔMCWD_r), standardised precipitation-evapotranspiration index (ΔSPEI_r) and vapour pressure deficit (ΔVPD_r), each one of these interacting with forest type, and accounted for soil characteristics by including in the models the CEC, pH, clay and sand content (maps in Fig. S3 to Fig. S8). Our results for the full community assemblage, survivor and for recruit and fatality assemblages (table S4) demonstrate the role of climate, specifically temperature and water availability, as a determinant of trait shifts across the forests, and show the differences in response between lowland and montane forests (table S4). Our mapped model predictions (maps in Fig. S3 to Fig. S8) depict in a spatially explicit way areas where stable CWM trait values (light yellow and light blue), their increases (darker blue) or decreases (yellow to red) are predicted to have occurred across tropical American forests with some of the strongest CWM trait shifts predicted across forests in Amazonia.

Can tropical American forest functional composition track climate change?

We next examined whether the observed community trait changes are sufficient to maintain expected trait-environment relationships for the full community, the survivor, and the recruit assemblages, based on spatial relationships between traits and climate. We expected recruitment to be more sensitive to climate change as the full community is dominated by the demographic inertia of established adult trees. To quantify the trait changes that would be necessary for forest communities to track predicted climate change, we first quantified the relationship between community traits and environment before most anthropogenic climate changes occurred (1980-2005; i.e., as baseline CWM trait-environment relationships). We took our observed trait-climate relationships (built with the 1980-2005 period data; table S5) and used them to predict the trait CWM to the 1980-2005 climate conditions plus the observed changes in climate across the study sites for the full time period (the last 40 years). This allowed us to predict the CWM trait values that the forests would have if they fully tracked recent climate change, assuming that trait-climate relationships are similar across space and time (table S6 and table S7). The ratio between the observed and the expected changes (for the full and the recruit assemblages) indicates how closely these forest traits are tracking our climate equilibrium predictions based on community changes alone (Fig. 6).

Our results show that for all measured traits of the survivor and full community assemblages, the community trait composition is not changing sufficiently to track climate change, with most changes being rather small and unlikely to represent important impacts on ecosystem functioning. However, the recruit community shows the largest shifts (Fig. 4, Fig. 6; results for all assemblages are in Fig. S9). At the region-wide scale for the survivor assemblages, all traits show less than 8% for lowland forests and 4% for montane forest of the change required to track climate. For the full community assemblage, all traits show less than 6% of the climate-predicted shifts in the expected direction for lowland forests and 7% for montane forest of the expected change (Fig. S9; table S6 and table S7). Several traits show very little change or even modest changes in the opposite direction to those expected (Fig. 6A and Fig. 6B). We detected larger community trait shifts in the recruit assemblages of an average 21.8% of the change required for lowland forests and 17.5% for montane forests when only traits shifting in the expected direction are considered. When both, shifts in the expected direction and in opposite direction, are considered, the recruit assemblage shows an average shift of 11.4% for lowland and -0.67% for mountain forests (Fig. 6C and Fig. 6D; table S6 and table S7). In lowland forests, community mean wood density appears to be changing fast enough in the recruit assemblages to track climate change expectation. Overall, we see some evidence of how the recruit forest assemblages of lowland and montane forests are shifting their community traits, often for different sets of community mean trait values, in response to climate change. However, for most traits even the recruit community does not seem to be changing quickly enough to track climate change. More significant community trait shifts have occurred in lowland than in montane forests, which is consistent with a more rapidly drying climate in lowland forests (Fig. 5; table S3).

Discussion

Overall, we find that 1) trait-environment relationships are similar for most of the studied traits across lowland and montane tropical American forests; 2) lowland forests show significant and larger changes in more community traits analysed than montane forests; 3) across the forests and for the full community and survivor assemblages, the abundance of deciduous species is increasing, with accompanying increases in leaf photosynthetic capacity and decreases in leaf area and leaf thickness, yet the recruit communities in the lowland forests have on average decreased in the abundance of deciduous species, leaf nitrogen content and wood density; and 4) crucially, for the full tree community and survivor assemblages most of these traits are changing at only a fraction of the rate required to maintain equilibrium with climate. Notably, the recruit communities show the best tracking of a changing climate.

The community trait shifts were similar for the survivor and full community assemblages and, although significant in several cases, these have been rather small over the past 40 years. In general, such community trait changes differed from those of the recruit and fatality assemblages. This is likely because the trait shift responses of the survivor and full community assemblages are dominated by large individuals that continued growing throughout the study period. Another potential explanation is that the survivor and full community assemblages, along with their concurrent functional trait composition, are still able to withstand the observed changes in climate. The survivor and full community assemblages have shifted towards more deciduous communities with higher photosynthetic capacity, leaf chemistry and adult maximum height. At the same time, we uncover a general decrease in leaf thickness for the survivor and recruit assemblages. Temporal increases in VPD have potentially favoured increases in the proportion of deciduous species, especially across montane forests, and increases in MCWD partially explain decreases in leaf thickness. Overall, deciduous species tend to have acquisitive leaf traits with higher leaf nitrogen and phosphorus, photosynthetic capacity and photosynthetic nitrogen-use efficiency, especially under water stress (*58)*, than evergreen species (*59, 60*). The pattern observed across tropical American forests could be attributable to leguminous nitrogen-fixing species that dominate in dry forests which are often deciduous and with higher photosynthetic nitrogen-use efficiency (*61*). This is consistent with a previous report for West African tropical forests, where increasing drought stress co-occurred with an increased abundance of deciduous species, and where changes in deciduousness explained changes in other morphological, structural and leaf chemistry traits (*56*). The abundance of deciduous species may be limited by soil fertility (*62*) in areas such as in south-eastern Amazonia (more so the Guiana Shield), where short-lived deciduous leaf construction is a too-costly strategy. Thus, increase in deciduousness is expected to be one adaptation strategy, especially in dry tropical forests with more seasonal precipitation regimes and nutrient rich soils than wetter tropical forests.

There is a mismatch in trait responses to climate change between the recruit assemblage and both the full community and survivor assemblages. This mismatch is most pronounced with respect to the abundance of deciduous species, leaf carbon, and adult maximum height. With increasing temperatures and reduced water availability, we expected an increase in abundance of deciduous species to also be reflected in the recruit assemblage (*56*). However, the decline in abundance of deciduous species in the recruit assemblage indicates potential shifts in phenological strategies towards more conservative strategies in response to increasing temperatures or altered precipitation patterns. The recruit assemblages also select for lower leaf carbon and species with shorter adult maximum heights. This finding suggests a decoupling in trait space between the functional trait characteristics of the mature forests we see in the present, and the possible future functional composition of tropical American forests. The selection for low leaf nitrogen in the recruit and fatality assemblages raises the question of whether and to what extent such recruit assemblages with low leaf nitrogen content will be able to survive to larger adult sizes (e.g. *58, 63*), especially across montane forests where there is a stronger mismatch. Such a decoupling in trait space between the recruit and survivor assemblages could potentially indicate the slow beginnings of forest-level adjustment to new climatic conditions, which is likely to impact the functioning of tropical forest ecosystems (*64*). We did not find a significant selection against deciduous species in the fatality assemblage. This suggests that a combination of drought avoidance and drought resistance strategies (*38*) could both be playing an important role as means of adaptation to a warming climate across lowland and montane tropical forests.

Other factors may be promoting the observed change in community-mean traits, such as species interactions and defaunation, the latter being a potentially important driver of changes in dispersal traits across time *(65)*. Some wetter regions (e.g., central Amazonia) show slight increases in seed mass for the full community (Fig. S4 D), with the fatality assemblage showing significant declines in individuals with smaller seeds in the lowlands (Fig. 5). However, drier regions (e.g., southern and eastern fringes of Amazonia) and montane forests show a slight predicted decline in seed mass (Fig. S4 D). These changes may be an indicator of defaunation pressure (*66*) as spatial predictions of decreases in seed mass broadly match spatial patterns of high defaunation (*67*), especially in those more accessible areas of Mesoamerica, and both south and eastern Brazil. They could also be driven by climatic factors as the observed changes are consistent with a shift from endozoochory (animal dispersal) to anemochory (wind dispersal), with the latter exhibiting smaller seeds than those dispersed by animals and being more prevalent in drier biomes *(42)*. Including other relevant traits, such as those related to hydraulics and thermal tolerance, and considering ecological interactions could further bring new evidence of these potential forest adjustments to a changing climate.

The survivor, full community and recruit assemblages often show more changes in traits in lowland than montane forest. Lowland forests are highly dynamic and harbour a high functional trait diversity that potentially allows for selection from a wider pool of trait values under climate stress. There has been a larger increase in atmospheric VPD in lowland forests than in montane forests, caused by more pronounced increases in temperature over the last 40 years, which could partially explain the shift of a larger number of community functional traits in lowland than montane forests (*68*). Larger increases in VPD and more severe droughts appear to have modified the community composition of lowland forests more strongly than that of montane forest, towards a set of species better adapted to drier and hotter conditions, which could be due to the mortality of more vulnerable species (*52*). Recent work across sites in the Amazon and Andes also suggest an important impact of increasing temperatures and declines in water availability on tree trait composition (*69*). We investigated the impact of macroclimate on the changes in functional trait composition of tropical forests. However, such macroclimate conditions may not directly mirror the microclimatic conditions found under the forest canopy such as temperature (*70*). This is of particular importance when investigating the effects of a changing climate, especially on the recruit assemblages, which tend to occupy the space below the canopies of the older larger trees. Ultimately, such microclimatic conditions may play an important role for determining the responses of understorey plants to a changing climate (*71, 72, 73*) and therefore on the rate of change in community trait composition of the recruit assemblages. Hence, microclimatic conditions at the plot level may partly explain the differences in trait shifts between the full community and survivor assemblages and the recruit assemblages.

It would mechanistically be expected that increasing drought would cause plant communities to shift to species with higher wood density and thicker leaves or that the abundance of deciduous species would increase across time. Such coordinated changes may not readily happen in the community as it is whole phenotypes that are changing, i.e. particular combinations of traits, rather than isolated traits. Moreover, coordination of different strategies could allow for alternative adaptations to the same drivers. For example, drier conditions might encourage deciduousness combined with low wood density and thin leaves (drought avoidance), or evergreenness combined with high wood density and thicker leaves (drought tolerance). The favoured combination(s) may depend on forest seasonality patterns and soil nutrients. Furthermore, not all trait combinations may be present in any given regional species pool, even in species-rich biomes, which may limit the shifts in community traits that can occur at any given time as a response to environmental change. Other factors may also contribute to trait shifts or a lack thereof across forest communities, such as soil conditions (*74*), biotic interactions (e.g., animal-plant interactions) (*75*) and wind disturbance (*76*). Our analyses represent community-wide responses mainly based on trait information at the species and genus level; traits may also express intraspecific plasticity that we are unable to assess here given the scale and multidecadal nature of the study. Some traits may show more or less plasticity than others and species intraspecific variation may contribute to adaptation to a changing climate (*77, 78)*. Overall, there is a lack of knowledge and data on the extent to which intraspecific trait variation plays a role in the adaptation of tree communities to a changing climate across the tropics. Here, we analysed only a set of relevant plant functional traits without adding information on intraspecific trait variation. Further research could focus on understanding responses of tree communities to climate change, including as much as possible information on intraspecific trait variation, and analysing other relevant traits. These could be hydraulic and thermal tolerance traits, which at the moment are not widely available for across tropical American forests.

In conclusion, we find that overall changes in community trait composition are leading to small shifts amounting to only ~10% of the expectation given climate change. These shifts are primarily driven by variation in growth rates of existing trees, rather than by recruitment or tree mortality. However, we observed larger changes for the recruit assemblage, directionally tracking climate at an average of 21%, which can potentially contribute to keeping these forests closer to, although still far from the equilibrium with climate. Trees are long-lived organisms with slow turnover rates compared to the rate of climate change and this partly explains the differences observed in community trait shifts between the full community and those of the recruit assemblages. There are specific areas where there seems to be a larger lag in forest responses to climate changes, especially in the Maya forest in Mesoamerica (*79*), and both the Atlantic forest and the southern Amazon forest in Brazil (*80*), which have become increasingly fragmented over time. Consequently, impacts of other disturbances across these regions, such as habitat fragmentation and in general a more constrained physical environment, may be impacting the capacity of forests to adjust to new climate conditions (*44, 81*). Our analysis demonstrates that tree community composition is shifting to track climate change, but that the overwhelming onus would have to be on within-species variability and trait plasticity (*82, 83*) to adequately track climate change. However, the changes in climate are likely to be too fast for adaptive phenotypic plasticity to keep track, especially in environments with low climatic heterogeneity (*82, 83*). Hence it is overwhelmingly likely that tree species composition and functional properties of tropical American forests (and probably all tropical forests) are increasingly out of equilibrium with local climate. Such disequilibrium almost certainly increases vulnerability to a further changing climate.

Summary of methods

Understanding trait CWM-Climate relationships and the effects of climate change for driving trait CWM changes

To understand the current trait-climate relationships across forests of the tropical Americas, for each plant trait we modelled the trait CWM as a function of climatic and soil covariates, with each one of the climatic variables interacting with forest type (lowland or montane) (here onwards referred to these models as M1)**.** We next analysed the climatic drivers of shifts in each functional trait given observed changes in climate over the past 40 years for the full community and survivor assemblages, for the recruit community and fatality community. The fatality community is defined as those individuals of a plot who were alive in a previous census but dead in the following census. We calculated the temporal changes in trait CWM at the plot level as the annual rate of change to standardise for a different time between censuses for different plots. We then modelled the Δr CWM trait as a function of Δr of the climatic variables described above, each one of these interacting with forest type and also included the soil characteristics (hereafter referred to these models as M2).

Understanding shifts in trait CWM

We used the annual rate of change (Δ*r*) of the trait CWM of the full, survivor, recruit and fatality community assemblages to investigate if the rate of trait changes for the overall forests (lowland and montane together), for the lowland forests alone and the montane forest alone, was significantly different from 0. We did the same to understand if there were important differences between the rate of change between lowland and montane forests. To this end we carried out a Bayesian version of a typical T-test analysis using Bayesian estimation (*84, 85*). As above, here we calculated the HDI containing the 95% most probable effect values and considered a result significant when the HDI did not overlap 0.

Understanding if forest community traits are tracking climate changes.

The process outlined below was carried out for the full community, the survivor and recruit assemblages only as the fatality ones are not tracking climate. We first built the same type of statistical models as M1 but using only plot and climatic data from between 1980 and 2005, including also the soil variables (from now on called M1.1). We used the M1.1 Trait-Environment statistical models and obtained predictions of the trait CWM to a new set of climatic conditions composed of the 1980-2005 climate plus the observed climate yearly rate of change across the study period (here onwards M2). We then calculated the difference between the trait CWM obtained with the M1.1 and M2 models to obtain the expected trait CWM change. Lastly, we compared the expected trait CWM calculated above with the observed Δ*r* CWM trait. This allowed us to understand the expected shift in mean trait values given the 1980-2005 trait-climate relationship in comparison to the observed trait changes across time (i.e., from 1980-2021). We tested for significant difference between observed and expected community trait changes using using Bayesian estimation (*84, 85*). We also created map predictions of the 1980-2005 M1.1 trait-climate model across tropical American forests by predicting this model to a climate change scenario that was composed of the observed climate (1980-2005) plus the yearly rate change observed. We then subtracted the original map predictions (those made with the M1.1 models without changes in climate conditions) to obtain the expected CWM trait changes at the pixel level (in the map) for across forests in tropical America. Then we calculated the ratio of the observed, i.e., spatial predictions of the trait changes observed across time (from M2 models), versus expected and converted to percentage change relative to the 1980-2005 condition to understand if and to what extent the observed trait changes are tracking (values above zero) or not (values of zero) the expected changes given the observed changes in climate or shifting in opposite direction than expected (values below zero).

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Data availability

The vegetation census and plant functional traits data that support the findings of this study are available from gem.tropicalforests.ox.ac.uk *(28)*, www.ForestPlots.net *(29),* and their other original sources. Given data sovereignty from the original data owners raw data on vegetation censuses across time are not publicly available but can be requested by contacting all researchers through the ForestPlots *(30)* data request protocol described in forestplots.net/en/join-forestplots/working-with-data. Raw climate data can be accessed through the TerraClimate database *(49)*. The SPEI data can be obtained from the SPEI database (*86*). The computer code used to reproduce the main findings in this manuscript *(87)* and the plot level processed data *(88)* are archived in the Zenodo repository (zenodo.org).

Supplementary Materials

Materials and Methods
Figs. S1 to S11
Tables S1 to S7
References *(35, 89-98)*

Figure legends

Fig. 1. Study area showing the distribution and number of vegetation plots sampled across time (A), principal component analysis (PC1, PC2 and PC3) depicting the climate and soil chemistry and texture space available in the study area (T_{mean}: mean air temperature, MCWD: maximum climatic water deficit, $SPEI_{12}$: standardised precipitation-evapotranspiration index, VPD: vapour pressure deficit, CEC: soil cation exchange capacity, soil pH, sand and clay amount) and the location of the sampling plots in the environmental space (B), and change in climate conditions (1980-1990 vs 2010-2020) in the plot network (C). In B) PC1 is mainly loaded by the maximum climatic water deficit (MCWD: -0.527) and Vapour Pressure Deficit (VPD: -0.515), PC2 by air temperature (T_{mean}: -0.465) and soil cation exchange capacity (CEC: 0.524) and PC3 by soil clay % (-0.535) and soil sand % (0.486). In C) the vertical dotted lines indicate zero change. Brown colours depict increases in temperature, drier conditions (for MCWD and VPD) or increased drought intensity (for SPEI: standardised precipitation evapotranspiration index). Blue colours depict an increase in water availability. In MCWD larger positive values indicate higher water stress. Climate data was derived from the TerraClimate project (*49*) and soil data from SoilGrids.org (*50*).

Fig. 2. Conceptual figure depicting the analysed mechanisms for change in community trait composition across the study area. Tree individuals that are alive and have a diameter at breast height equal or above 10 cm are part of the full community assemblage. Across time, there can be changes in the community trait composition due to growth of the surviving tree individuals (Survivor assemblage) given their increase in basal area (top right). Other mechanisms for changing community trait composition across time are the recruitment (Recruit assemblage) of new individuals (middle right) and the death (Fatality assemblage) of individuals in the community.

Fig. 3. The relationship between community-mean plant traits and temperature. Trait-environment relationships for mean annual temperature (T_{mean}) across the vegetation plots. Thick blue (for lowland forests) and yellow (for montane forests) lines show the average trait response to the climatic variable, with gray-shaded lines show 700 random draws from the model posterior distribution representing the variability of the expected model fit. Trait-environment relationships for maximum climatic water deficit ($MCWD_{mean}$), vapour pressure deficit (VPD_{mean}) and standardised precipitation-evapotranspiration index ($SPEI_{mean}$) are shown in Figure S2. For full statistical multivariate model results see table S2**.** A_{sat}: photosynthetic capacity at light-saturation, C: leaf carbon content, N: leaf nitrogen content, P: leaf phosphorus content, Area: leaf area, Fresh mass: leaf fresh mass, SLA: specific leaf area, Thickness: leaf thickness, DE: deciduousness, H_{max}: adult maximum height, WD: wood density, Seed mass: mass of the seed.

Fig. 4. The analysed Survivor (top panel), Recruit (middle panel), and Fatality (bottom panel) assemblages in the study. In each panel, the highlighted vegetation represents the specific assemblage under analysis. Each panel provides a summary of observed changes in community traits and the percentage of climate tracking by each assemblage, with exception of the Fatality assemblage for which climate tracking is not possible.

Fig. 5. Estimated changes in mean community functional trait values across time for tropical American forests. All traits with their spatial prediction maps are shown in Figs. S3 to S8. A) Changes in trait community-weighted mean (CWM) for leaf photosynthetic capacity and leaf chemistry traits, B) for leaf morphology and structural traits and C) for tree phenology

and structural traits. Each panel shows the observed yearly rate of change, obtained from sampled vegetation plots, from the statistical models in table S3 for all forests together and only for lowland or montane forests for the survivor (blue), recuit (green) and fatality (gray) assemblages. Significant shifts are shown as filled circles and non-significant as empty circles. The vertical lines depict the Highest Density Intervals (95% HDI), and the horizontal grey dotted line indicates zero change. A_{sat}: photosynthetic capacity at light saturation, C: leaf carbon content, N: leaf nitrogen content, P: leaf phosphorus content, Area: leaf area, Fresh mass: leaf fresh mass, SLA: specific leaf area, Thickness: leaf thickness, DE: deciduousness, H_{max}: adult maximum height, WD: wood density, Seed mass: mass of the seed.

Fig. 6. Tracking of trait community weighted mean (CWM) for the survivor (A, B) and recruit (C, D) assemblages in lowland (A, C) and montane (B, D) forests given the observed changes in climate across the sampling plots. The X axis shows the ratio of changes in trait CWM, based on actual trait CWM changes observed at the plot level through time, versus expected changes in trait CWM, based on spatial climate-trait relationships given observed changes in climate. Positive values (black bars) indicate that observed and predicted changes are both positive or both negative and, hence, are going into the same direction, whereas negative values (grey bars) indicate that observed and predicted changes are going in opposite directions. A ratio of change value of one would indicate perfect tracking. The Y axis shows the traits sorted by the change ratio amount (see full statistical details in table S6 and table S7). Values of zero and close to zero represent no or slight trait shifts. A_{sat}: photosynthetic capacity at light saturation, C: leaf carbon content, N: leaf nitrogen content, P: leaf phosphorus content, Area: leaf area, Fresh mass: leaf fresh mass, SLA: Specific leaf area, Thickness: leaf thickness, DE: deciduousness, H_{max}: adult maximum height, WD: wood density, Seed mass: weight of the seed.